

# THE PHYLOGENETIC SYSTEM OF THE GAYELLINI (HYMENOPTERA: VESPIDAE; MASARINAE)\*

BY JAMES M. CARPENTER

Museum of Comparative Zoology, Harvard University,  
Cambridge, MA 02138

## INTRODUCTION

The Gayellini is one of the two tribes of Masarinae (Carpenter, 1981). Endemic to the Neotropics, the majority of the species are Patagonian, but one ranges as far north as Mexico. With ten described species, the group is far less speciose than its sister-tribe Masarini, which has over 200 described species (*cf.* Richards, 1962), and most species are rarely collected. These wasps have a very distinctive appearance among Vespidae (Fig. 1), and their taxonomic history has been more turbulent than any other higher vespid taxon. Although the phylogenetic placement of the group as a whole has now evidently been settled (Carpenter, 1981), no study has been made of the species. The current generic classification is fragmented, and there have been no keys to all of the taxa. In this paper, I investigate the phylogenetic relationships of the species, and present a revised generic classification along with keys to all taxa.

## TAXONOMIC HISTORY

Saussure (1852-58) placed *Gayella* in the Section "Anomaloptères" of the "Euméniens" because the forewing recurrent veins ( $m-cu_{1-2}$ ) are received in separate cells (Fig. 6), as in the other genera placed in this section (*Raphiglossa*, and *Stenoglossa* = *Psiloglossa*). In other vespids he studied both veins were received by the second submarginal cell. Ashmead (1902a) described the subfamily Raphiglossinae (in his Eumenidae) for this group, but by that time other genera had been described which had the diagnostic character of the recurrent veins. These were *Euparagia* and *Paramasaris*, both considered probable masarines by their authors (Cresson, 1879, and Cameron, 1901, respectively). Ashmead (1902b) proposed the tribe Euparagiini in his Masaridae for these two genera. So the recurrent

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veins were no longer uniquely diagnostic. Bequaert (1918) questioned whether *Gayella* belonged in the Raphiglossinae, since the longitudinal plaiting of the forewings "is very obsolete" in the genus, and Bradley (1922) placed it in its own subfamily in Vespidae *s. l.* Bequaert (1928) transferred *Paramasaris* to this subfamily, based on its possession of the characteristic hindwing venation of *Gayella* (Fig. 3). Richards (1962) included the Gayellinae in his Masaridae, but his dendrogram showed Euparagiinae as more closely related to the subfamily Masarinae. I (Carpenter, 1981) demonstrated that Richards' Masaridae was a paraphyletic group, since Euparagiinae is the sister-group of Vespidae as a whole. Four synapomorphies were adduced which showed a sister-group relationship between gayellines and masarines: presence of hypostomal apodemes, loss of the midfemur basal ring, loss of the scutal lamella and provisioning with nectar and pollen. Gayellines and masarines were treated as tribes in an expanded Masarinae, the system followed here.

*Gayella* was originally described as monotypic for *G. eumenoides* by Spinola (1851). Saussure (1855 in Vol. 3 of *Études*), Willink (1956, 1963) and Willink and Ajmat de Toledo (1979) added five species. The latter paper provided a key to the six species, however I believe that the key given here will be easier to use. *Paramasaris* was also originally described as monotypic, for *P. fuscipennis* Cameron. Cameron (1904) later described a new genus *Zethoides* (non *Zethoides* Fox, 1899; *Plesiozethus* Cameron, 1905, and *Metazethoides* Schulz, 1906, are replacement names) for *Z. flavolineatus*, which differed from *Paramasaris* in having only two (Fig. 5), as opposed to three (Fig. 6), submarginal cells. Zavattari (1912) questioned whether Cameron had described this character correctly, and Bradley (1922) suspected that *Plesiozethus* was a synonym of *Paramasaris*. This was confirmed by Bequaert (1928), who showed that the number of submarginal cells was variable, and synonymized *flavolineatus* with *fuscipennis*. Giordani Soika (1974) described two new species in the genus, but provided no key. He also described a new genus, *Paragayella*, monotypic for the new species *Paragayella richardsi*. I consider this genus a synonym of *Paramasaris*, as discussed below. I also give the first key to species of the group.

#### MATERIALS AND METHODS

All of the species have been examined. Types of *Paramasaris* have been seen; treatment of *Gayella* follows Willink's concepts. Com-

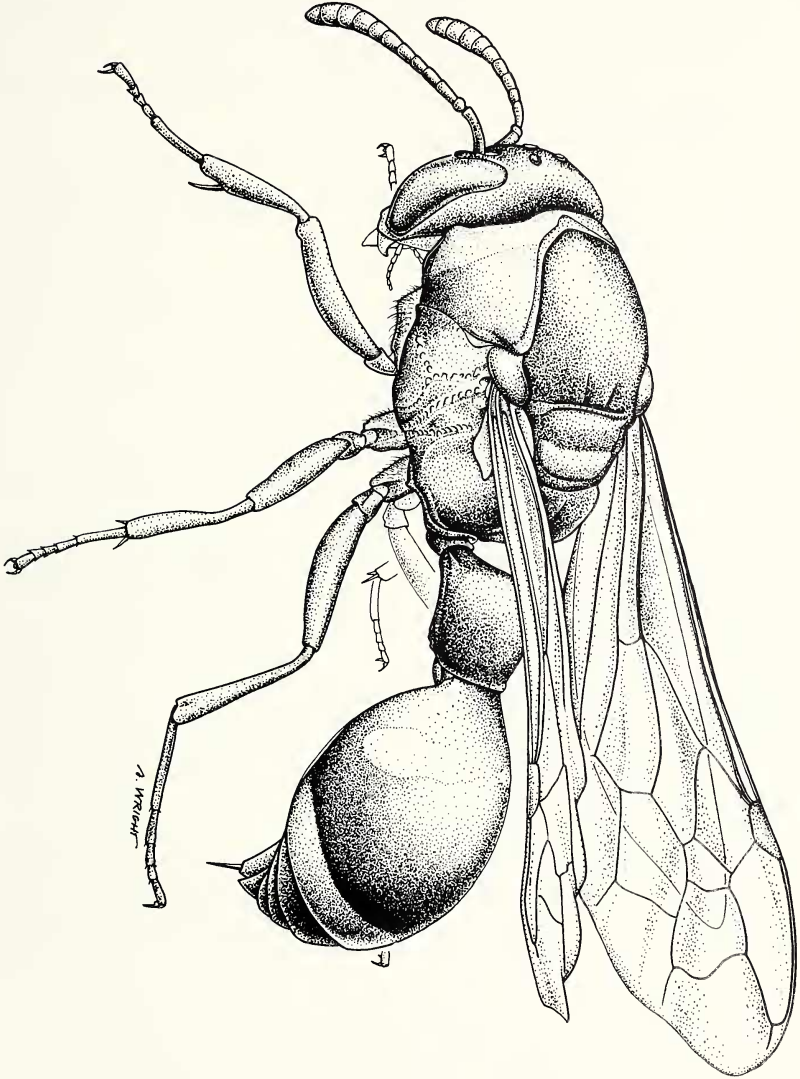


Fig. 1. *Gayella eumenoides*, ♀.

plete label data for all material of *Paramasaris* are listed under taxonomic notes for each species; for the relatively better known *Gayella* only provinces are noted. Acronyms for collections are listed below, along with the name of the individuals who provided the material where this was borrowed.

- AMNH American Museum of Natural History, New York  
(M. S. Favreau)
- BMNH British Museum of Natural History, London (M. C. Day, C. R. Vardy)
- CAS California Academy of Sciences, San Francisco (W. J. Pulawski)
- CP Charles Porter personal collection
- IML Instituto Miguel Lillo, Tucuman (A. Willink)
- IPC Instituto Pedagógico de Chile
- MCZ Museum of Comparative Zoology, Cambridge
- MF M. A. Fritz personal collection
- MNHN Muséum National d'Histoire Naturelle, Paris
- UCD University of California, Davis (P. S. Ward)
- USNM U.S. National Museum of Natural History, Washington  
(A. S. Menke)

Morphological terminology follows Carpenter (1981), except that I have adopted Snelling's (1986) more descriptive terms "preoccipital" and "postocular" for the carinae previously termed "dorsal occipital keel" and "ventral occipital keel" (Richards, 1962). Detailed examination of the labiomaxillary complex and male genitalia was made by dissection of these structures, clearing slightly in cold lactophenol, and examination in glycerin. Measurements were made with an ocular micrometer. Illustrations were made with a Wild M-400 photomicroscope employing Kodak TMAX 400 film. Cladistic analysis (Hennig, 1966) was performed for all the features discussed in this paper. Outgroup taxa include Masarini and Euparagiinae, with reference to other Vespidae also occasionally made.

## RESULTS

### *Subfamily characters*

First I discuss some morphological features important in higher-level vespid relationships, before turning to consideration of the phylogenetic relationships among the species. Autapomorphies of

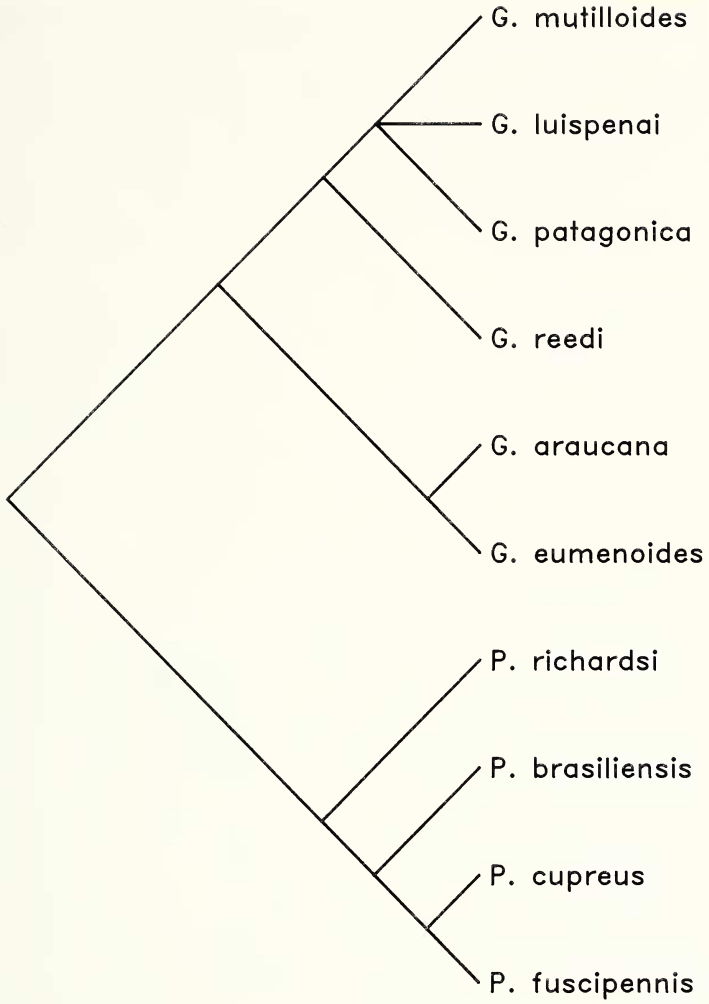


Fig. 2. Cladogram of the species of Gayellini.

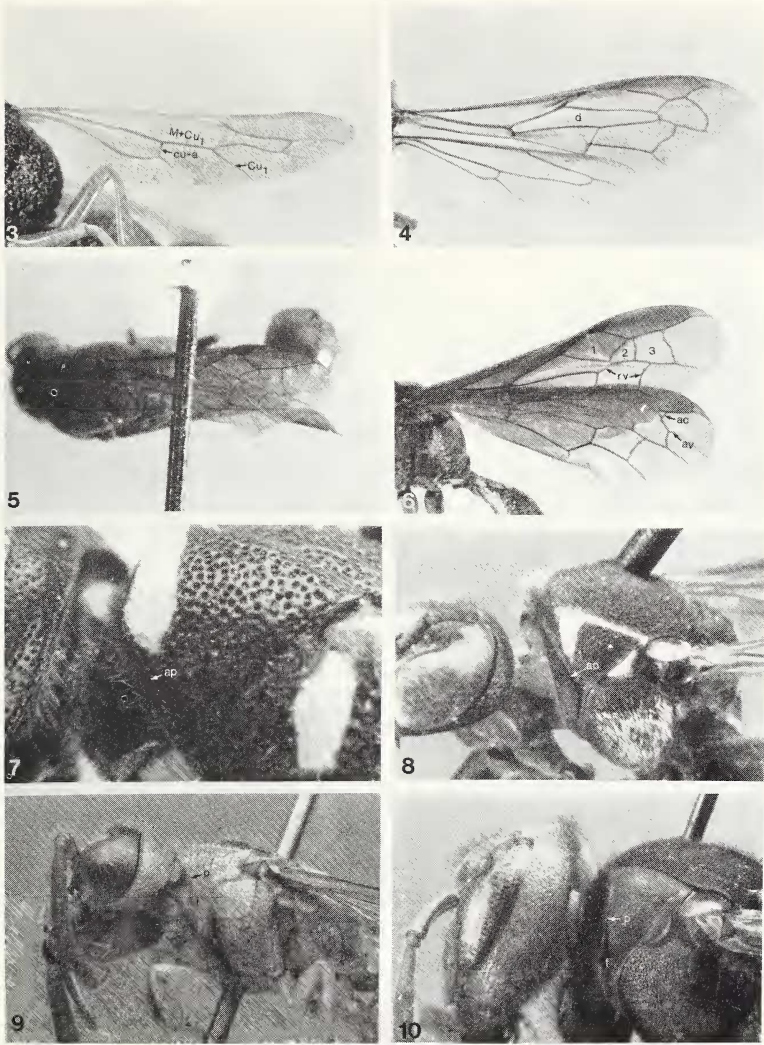
the Gayellini listed by Carpenter (1981) include the hindwing with  $Cu_1$  diverging from  $M+Cu_1$  far distad of the insertion of  $cu-a$  (Fig. 3), the clypeus with the dorsal margin bisinuate (Fig. 12), the first metasomal tergum and sternum fused and metasomal segments after II retractile (the latter two convergent with other vespids). Some other autapomorphies are mentioned below.

*Forewing discal cell.* Carpenter (1981:14) noted that the discal cell is shorter than the submedian in *Paramasaris*. This is also the case in *Gayella* (Fig. 1), and this should be considered a reversion from the state of an elongate discal cell in other Vespidae (Fig. 4; cf. Carpenter, 1981), and thus an autapomorphy of Gayellini.

*Forewing radial region.* The variation in the number of submarginal cells in *Paramasaris* was alluded to above. Besides *fuscipennis*, I have seen loss of  $r-m_2$  producing two submarginal cells in several specimens of *brasiliensis* (including the allotype and paratype, Fig. 5). The placement of  $m-cu_1$  varies as well, sometimes meeting  $M$  at the fork where  $RS$  diverges. But this is not correlated with number of cells, and most specimens have the usual condition of  $RS$  diverging first (Figs. 5-6). In addition, the specimen of *Paragayella richardsi* from Formoso, Brazil, has a very small adventitious cell at the junction of  $r-m_3$  and  $RS$  on one wing (Fig. 6), and both Goias specimens have an adventitious vein spur arising from the middle of  $r-m_3$  (Fig. 6).

*Clypeus.* The clypeus is narrower than its height in all species, particularly in males (Figs. 11-17). Richards (1962:46) stated that the reverse is true in *Paramasaris*, perhaps a *lapsus*. This is not the usual state in Vespidae, and is perhaps apomorphic, although the degree of narrowing varies in the tribe.

*Occipital carinae.* Gayellini have both the postocular and preoccipital carinae in the groundplan, contrary to Richards (1962:12). The postocular carina is reduced in length, and may be present only as a trace just ventral to the eye in *Gayella*, but is typically obvious in the *eumenoides* group. The carinae are almost confluent in many specimens of *eumenoides* and *araucana*, separated by only a slight gap (Fig. 18). The "complete" carina in *Paramasaris* (Richards, 1962:46; Fig. 19) is evidently produced by confluence of the postocular with the preoccipital carina, as occurs in some Masarini (Snelling, 1986) and probably other Vespidae (Carpenter, 1988). The postocular carina is effaced in *Paragayella* (Fig. 20).



Figs. 3-10. 3. *Gayella araucana*, 7 $\times$ . Hindwing. 4. *Paragia decipiens aliciae*, 4 $\times$ . Wings. 5-6. Wings, 6 $\times$ . 5. *Paramasaris brasiliensis*. 6. *P. richardsi*. Submarginal cells are numbered. 7-10. Lateral view of pronotum. 7. *G. araucana*, 17 $\times$ . 8. *Euparagia scutellaris*, 10 $\times$ . 9. *Ischnocoelia robusta*, 6 $\times$ . 10. *Vespa affinis*, 5 $\times$ . ac: adventitious cell; ap: anterior pronotal carina; av: adventitious vein; d: discal cell; f: pronotal fovea; p: pronotal carina; rv: recurrent veins.

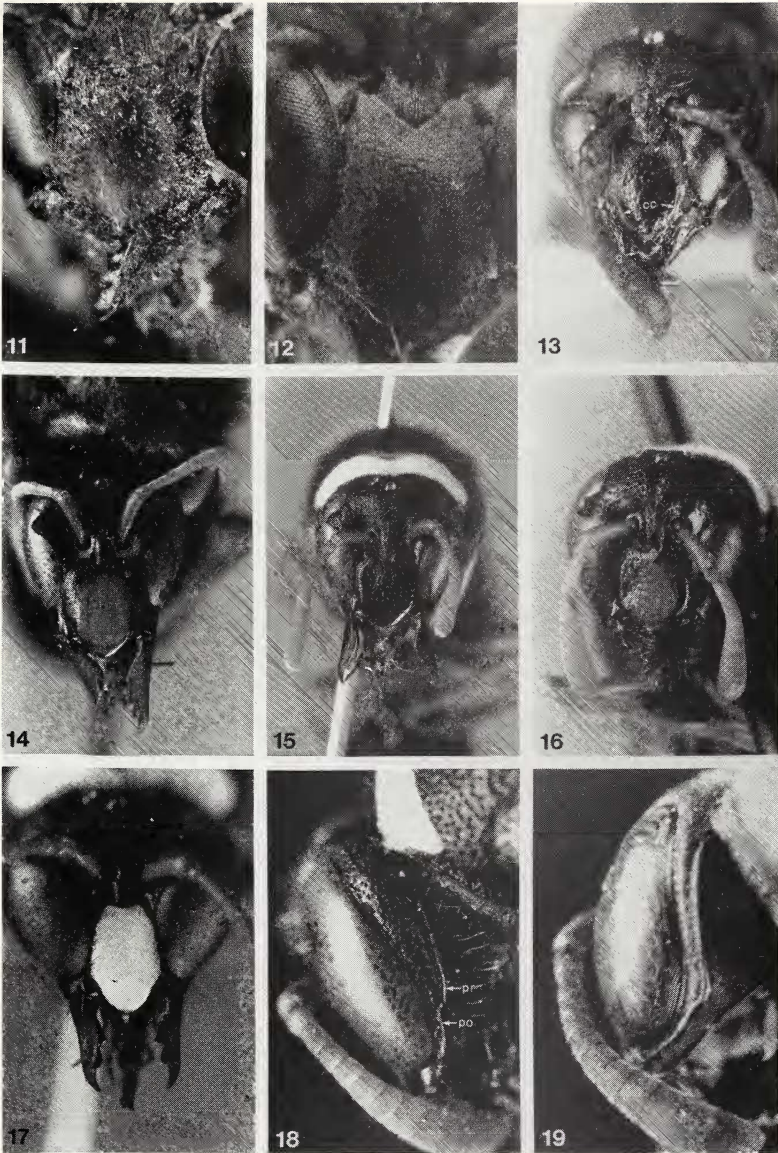
*Acroglossal buttons.* As noted by Carpenter (1981), Richards (1962) incorrectly stated that acroglossal buttons are lacking from the ligula of Gayellini. The only species in which they are entirely lacking are *Paramasaris fuscipennis* and *cupreus* (Fig. 21). These structures are also absent from the glossa of *Paramasaris brasiliensis*, but are present on the paraglossae. This is a transformation series in reduction. Other gayellines have the buttons on both the glossa and paraglossae (Fig. 22), including *Paragayella richardsi*, the sister-group of *Paramasaris*, and *P. brasiliensis* is the sister-group of *fuscipennis* + *cupreus* (Fig. 2).

*Hypostomal apodemes.* These are present in all species, which supports the interpretation of synapomorphy with Masarini. They are always very narrow (Fig. 23).

*Pronotal carina.* *Paramasaris* and *Paragayella* are notable for having two parallel carinae on the pronotum. One is present at the anteroventral margin of the pronotum; the other is posterior to this and runs towards the humeri and dorsum of the pronotum (Figs. 29–31, 40). The second carina shows a transformation series in development, ranging from short lateral sections only (*Paragayella*, Figs. 24, 29), to extending to the dorsum (*Paramasaris brasiliensis*, Figs. 25, 30), to complete across the dorsum (*P. cupreus* and *fuscipennis*, Fig. 26). This series apparently corresponds to the phylogenetic relationships among these species (Fig. 2). *Gayella* has only the anterior carina (Fig. 7). Euparagiinae also has only the anterior carina (Fig. 8), although the humeri are somewhat raised in *scutellaris*. In Masarini the anterior carina is usually blunt, and a lateral carina on the humeri may be present (Fig. 37). In all these groups, the anterior carina precedes a groove which is frequently crenate (secondarily reduced in various Masarini).

The situation is different in other Vespidae. In Polistinae, the structure termed the "pronotal prominence" (Richards, 1978) is probably homologous with the anterior carina. Although often blunt, it is frequently carinate, and lies at the anteroventral margin of the pronotum (Fig. 38). It precedes the pronotal fovea, which is sometimes set in a deep depression; there is no lateral groove. In the groundplan, there is also a carina on the dorsum (Carpenter, 1989). This second carina is usually quite short laterally, and may closely approach the anterior carina (Fig. 38). In *Polistes* the second carina extends almost to the ventral pronotal margin in many species, and the fovea, which is anterior to this carina, is not preceded by a





Figs. 11-19. 11-12. Clypeus, ♀. 11. *Paramasaris richardsi*, 19X. 12. *P. brasiliensis*, 27X. 13-16. Frontal view of head, ♀. 13. *P. cupreus*, 14X. 14. *Gayella mutilloides*, 5X. 15. *G. eumenoides*, 7X. 16. *G. araucana*, 10X. 17. *G. reedi* ♂, 10X. Frontal view of head. 18-19. Lateral view of head. 18. *G. araucana* 15X. 19. *P. brasiliensis*, 21X. cc: apical clypeal carinae; g: gap between mandibular teeth; po: postocular carina; pr: preoccipital carina.

“prominence” (Fig. 39). Richards (1973) confused the dorsal carina in *Polistes*, behind the fovea, with the anterior carina in other polistines, in front of the fovea. Eumeninae, which also have a fovea, also have a carina in front of the fovea (Fig. 9), which continues across the *dorsum* in the groundplan (Carpenter and Cumming, 1985). The single carina may be a composite structure, derived from a state resembling certain polistines with two closely approximated carinae (Fig. 38). This is also the case in the groundplan of Vespinae (Carpenter, 1987), where there is a single carina, preceding the pronotal fovea and running across the *dorsum* (Fig. 10). Stenogastrinae have a highly modified pronotum and lack a posterior carina and fovea (Carpenter, 1988), but have a blunt ridge anteriorly that may correspond to the anterior carina (Fig. 32).

Thus, an anterior carina is clearly an ancestral vespid character, but considering its diverse form, the posterior carina may have evolved multiple times. The alternative interpretation, that it evolved once (in the ancestor of all vespids except Euparagiinae), requires secondary losses within Gayellini (*Paragayella*, *Paramasaris* and *Gayella* independently) and Stenogastrinae. The interpretation of nonhomology is more parsimonious, and accords with the apparent transformation series in *Paramasaris*. In any case, the separate posterior carina has also been lost on numerous occasions within the Masarini and Polistinae (Carpenter, 1989, and in prep.), and the possibly composite carina has also been lost several times within Eumeninae and Vespinae (Carpenter, 1987; Carpenter and Cumming, 1985). Secondary loss also applies to the pronotal fovea, present in the groundplan of Eumeninae, Polistinae and Vespinae. It has been lost multiple times within Polistinae (Richards, 1978; Carpenter, 1989), and probably also in Stenogastrinae. Presently available morphological and behavioral evidence supports a sister-group relationship between Stenogastrinae and Polistinae + Vespini-

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Figs. 20–28. 20. *Paramasaris richardsi*, 17X. Lateral view of head. 21–22. Ventral view of ligula. 21. *P. fuscipennis*, 25X. 22. *Gayella luispenai*, 16X. 23. *G. mutilloides*, 14X. Ventral view of head, mouthparts removed. 24–28. Dorsofrontal view of pronotum. 24. *P. richardsi*, 9X. 25. *P. brasiliensis*, 11X. 26. *P. cupreus*, 13X. 27. *G. eumenoides* ♂, 10X. 28. *G. araucana* ♀, 8X. *ab*: acroglossal buttons; *ap*: anterior pronotal carina; *gl*: glossa; *h*: hypostomal apodeme; *hp*: humeral projection; *pg*: paraglossa; *plp*: posterior lingual plate; *pp*: posterior pronotal carina; *pr*: preoccipital carina.



nae (Carpenter, 1981, 1988, 1989), thus requiring an inference of loss in Stenogastrinae.

*Hind coxal carina.* Richards (1962) made contradictory statements concerning the presence of this feature in Gayellini (cf. p. 15 and 44). This was initially followed by Carpenter (1981), but corrected by Carpenter and Cumming (1985:907). All Gayellini lack this carina, a primitive condition.

*Claws.* Richards (1962:44) erroneously characterized the claws of *Gayella* as simple, and Carpenter (1981:26) initially followed this (corrected in Carpenter and Cumming, 1985:907). In fact, the claws are toothed in all species of Gayellini (variable in *G. mutilloides*). This is the plesiomorphic condition in Vespidae.

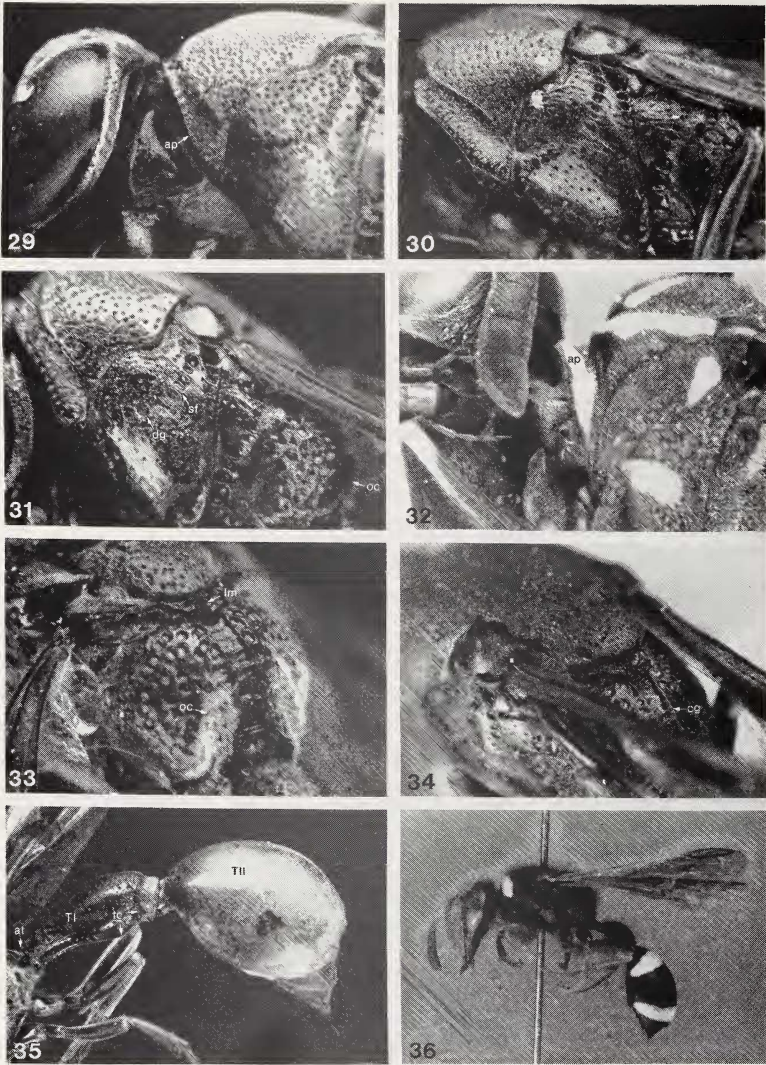
*Male genitalia.* I have examined the genitalia of all species except *Paramasaris cupreus* and *Paragayella richardsi*, where the males are still unknown. In the groundplan of the tribe, the aedeagus is broadly rounded apically, the digitus is a prominent triangular lobe that is desclerotized ventrally, the cuspis is a small lobe completely fused to the lamina volsellaris, and the parameral spines are long and sharply pointed (Figs. 56–63). Figure 39 of Richards (1962), showing a large, triangular cuspis and rounded digitus in *Gayella araucana*, is incorrectly labelled. What is there termed cuspis is actually the digitus, and the structure labelled as digitus must be the aedeagus (cf. Fig. 58). This figure was the reason I previously was unable to characterize the groundplan of the volsella in the tribe (Carpenter, 1981:26), as I had not seen that species at the time. Within genera, the genitalia are relatively uniform, with species differing in details (especially of the volsella); however, there are some consistent differences between the genera. These are discussed below.

### *Paramasaris*

Giordani Soika (1974) characterized *Paragayella* as related to *Gayella*, and stated (my translation): “This genus appears at first sight a *Gayella* by the general aspect and dimensions.” The type material I have seen he even labelled as “*Gayella richardsi*.” In fact, *Paragayella* is not really even superficially similar to *Gayella*. *Paragayella* lacks some of the apomorphies shared by the species of *Paramasaris*, and for some other derived traits which *Paramasaris* and *Paragayella* share the latter has a less developed state. Thus it shares some primitive similarity with *Gayella*, which of course indi-

cates nothing about phylogenetic relationship (Hennig, 1966). On the other hand, *Paragayella* shares several clear synapomorphies with *Paramasaris*. These include the forewing with r-m<sub>3</sub> more or less straight (Figs. 5–6; sinuous in *Gayella* and other Vespidae, Figs. 1, 4), the pronotum with two carinae (Figs. 29–31, 40; one in *Gayella* Fig. 7), the metanotum with a longitudinal median carina (Figs. 33, 46; none in other Masarinae), and the metasoma petiolate (tergum I in dorsal view at least twice as long as wide and half the width of tergum II, Figs. 35, 40–41; it is differently shaped in Euparagiinae, Masarini and *Gayella*, Figs. 1, 43–45). *Paragayella* is the sister-group of *Paramasaris*. Autapomorphies of *Paragayella* include the reduced postocular carina (Fig. 20) and the transversely carinate metanotum (Fig. 46).

The three species of *Paramasaris* share numerous synapomorphies. The postocular and preoccipital carinae are apparently confluent (Fig. 19). These carinae are separated in other Gayellini, and the postocular carina reduced in several species (*Paragayella*, the *Gayella mutilloides* group). The mandibles are tridentate with the proximal teeth separated from the apical one by a gap (Fig. 13). The mandibles are quadridentate in females of *Paragayella* and *Gayella* (Figs. 11, 14–15), and tridentate in males of the latter (Fig. 17; Richards, 1962:44, erroneously characterized the mandibles of *Paramasaris* as quadridentate and those of *Gayella* as simple); there is no gap. Quadridentate mandibles is the groundplan state of most of the Vespidae (Carpenter, 1981), although Euparagiinae has bidentate mandibles. The glossa is shortened and lacks acroglossal buttons, the paraglossae are broadened, and the posterior lingual plate is cordate in shape (Fig. 21). The posterior lingual plate is slightly broadened in other gayellines, but the length of the structure still exceeds its width (Fig. 22). The clypeus is broadly truncate (Fig. 12), which is here treated as derived, convergent with the groundplan of Masarini. *Paragayella* has the clypeus narrowly truncate (Fig. 11), as in Euparagiinae, which is considered the primitive state. A broad truncation seems most simply interpreted as derived from a narrow emargination, as does the pointed clypeus of *Gayella* (Figs. 14–17). The posterior carina of the pronotum extends further dorsad in *Paramasaris* (Figs. 25–26) than *Paragayella* (Fig. 24), a further apomorphic development. The propodeum has oblique carinae more or less developed (Figs. 31, 33), a unique trait in



Figs. 29-36. 29-32. Lateral view of pronotum and mesepisternum. 29. *Paramasaris richardsi*, 13 $\times$ . 30. *P. brasiliensis*, 14 $\times$ . 31. *P. fuscipennis*, 17 $\times$ . 32. *Parischnogaster mellyi*, 16 $\times$ . 33-34. Oblique lateral view of propodeum. 33. *P. fuscipennis*, 17 $\times$ . 34. *P. cupreus*, 15 $\times$ . 35. *P. brasiliensis* holotype, 9 $\times$ . Lateral view of metasoma. 36. *Gayella reedi* ♂, 3 $\times$ . Lateral view. *ap*: anterior pronotal carina; *at*: anterior truncation of metasomal tergum I; *cg*: carina delimiting

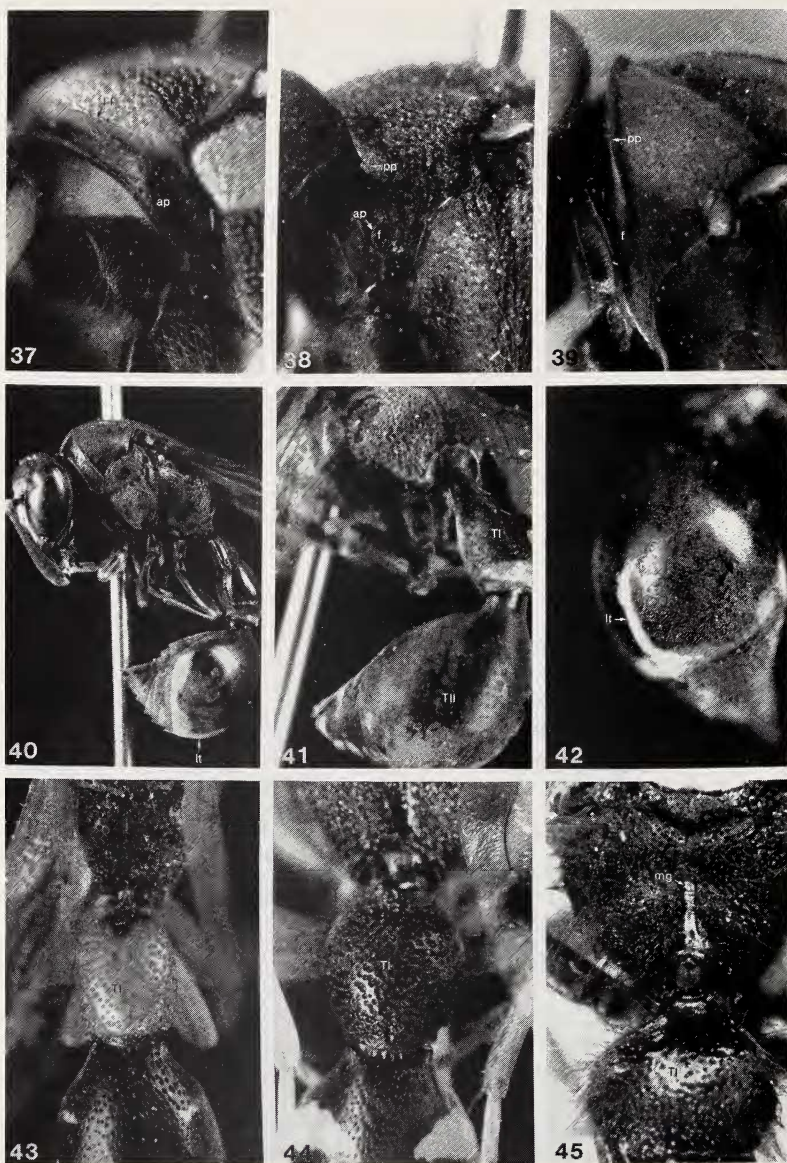
Masarinae. The first metasomal tergum has a blunt posterior ridge that is continued anterolaterally and drawn out into projections posterolaterally (Figs. 35, 40), a feature unique in Vespidae. The tergum is also strongly truncate anteriorly (Fig. 35). The second tergum has a median longitudinal ridge (Figs. 40, 42), which however is variably developed in *brasiliensis* (strong in the male and not developed in the female, Fig. 35). A longitudinal ridge is found elsewhere in Vespidae only within Eumeninae (*Cyphomenes*, where it is anterior). Finally, the parameral spines of the male genitalia are extremely elongate in *brasiliensis* and *fuscipennis*, being longer than the parameres and extending far beyond the apex of the aedeagus (Fig. 56). This is apparently a derived condition; in *Gayella*, Euparagiinae and Masarini the spines are shorter than the parameres and extend little beyond the aedeagus (Figs. 57–63). Males of *cupreus* are predicted to share this synapomorphy, and possibly also *Paragayella*.

Within *Paramasaris*, *cupreus* and *fuscipennis* are sister-groups. This is shown by the paraglossae also lacking acroglossal buttons (Fig. 21), the female clypeus with a pair of short apical carinae (Fig. 13), the second carina of the pronotum more complete dorsally (Fig. 26), and the longitudinal carina on tergum II well developed in females (Figs. 40, 42). Autapomorphies of the species are: for *cupreus* the propodeal median groove delimited by more lamellate carinae (Fig. 34); for *fuscipennis* the oblique propodeal carina better defined (Fig. 33), and the dorsal groove and scrobal furrow of the mesepisternum broader and deeper (Fig. 31, *cf.* with 29–30, 40). I have not discovered any autapomorphies of *brasiliensis*.

Since *Paragayella* is the sister-group of *Paramasaris*, recognition of both genera is consistent with monophyly. However, it serves little useful purpose. *Paragayella* itself has few apomorphies—it mostly lacks those of *Paramasaris*. Recognition of *Paragayella* thus contributes little to the process of efficient diagnosis. Since *Paragayella* is monotypic, and *Paramasaris* consists of but three

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propodeal median groove; *dg*: dorsal groove; *lm*: longitudinal metanotal carina; *oc*: oblique propodeal carinae; *pp*: posterior pronotal carina; *sf*: scrobal furrow; *TI*: metasomal tergum I; *TII*: metasomal tergum II; *tc*: posterolateral tergal projection.



Figs. 37-45. 37-39. Lateral view of pronotum. 37. *Metaparagia doddi* holotype, 13X. 38. *Parachartergus apicaloides*, 13X. 39. *Polistes anduzei*, 10X. 40. *Paramasaris cupreus* 6X. Lateral view. 41. *P. richardsi*, 8X. Oblique dorsal



species, recognition of *Paragayella* is but another example of the current needless fragmentation of vespid generic classification, which I have decried elsewhere (Carpenter and Cumming, 1985; Carpenter, 1987, 1988). A fully sequenced cladistic classification (Wiley, 1979) is possible with a single genus. I am therefore synonymizing *Paragayella* with *Paramasaris*.

### *Gayella*

The monophyly of the genus is shown by the pointed clypeus (Figs. 14–17; not similar to that of Stenogastrinae and Polistinae), the temples projecting somewhat and the emarginate and bispinose last metasomal tergum (Figs. 50–52). In other Masarinae and Euparagiinae the clypeus is truncate or emarginate, the temples do not project and the last visible metasomal tergum is neither emarginate nor spined. Several characters of the male genitalia are also synapomorphies. The digitus is enlarged relative to *Paramasaris* (cf. Figs. 56 and 57–63), the cuspis is tuberculate basally (Figs. 57–61, 63), and the paramere has an enlarged lobe (*dorsal* to the spine, Fig. 62). The combination of features of the male genitalia is unique in Vespidae. Finally, the globose shape of the first metasomal tergum may be apomorphic, but this is variable within the genus (Figs. 43–45).

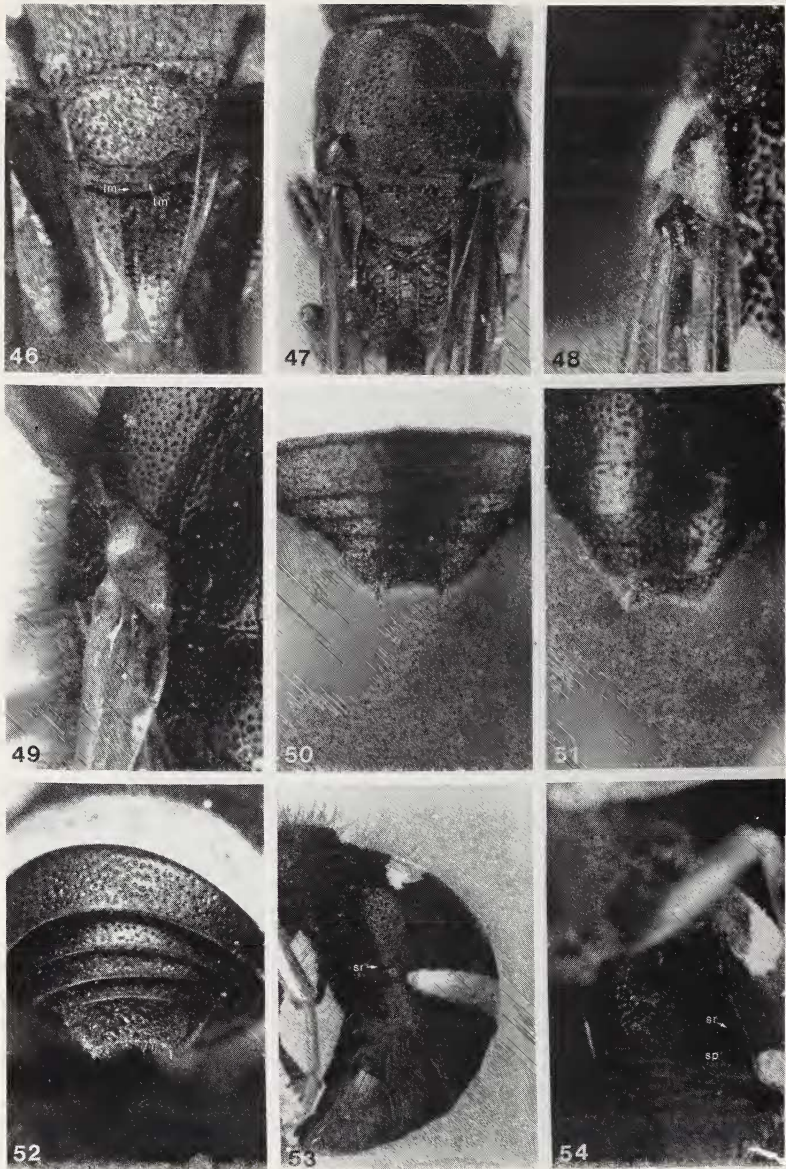
Within the genus, two monophyletic species groups may be recognized, which allows a classification that is phylogenetically sequenced (Wiley, 1979). These are the *eumenoides* group, for *eumenoides* and *araucana*, and the *mutilloides* group, including *reedi*, *patagonica*, *luispenai* and *mutilloides*.

### *Eumenoides* group

The monophyly of the *eumenoides* group is established by the tegula, which lacks the short posterior lobe found in *Paramasaris* and the *mutilloides* group (cf. Figs. 47 and 48). This feature is approached in *reedi* (Fig. 49), diminishing its strength. The projection from the cuspis is tuberculate and apical relative to that

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view of metasomal terga I and II. 42. *P. fuscipennis*, 13X. Lateral view of metasomal tergum II. 43–44. Dorsal view of ♂ metasomal tergum I, 10X. 43. *Gayella araucana*. 44. *G. eumenoides*. 45. *G. luispenai* ♀, 10X. Posterodorsal view of propodeum and metasomal tergum I. *ap*: anterior pronotal carina; *f*: pronotal fovea; *lt*: longitudinal carina of metasomal tergum II; *mg*: propodeal median groove; *pp*: posterior pronotal carina; *TI*: metasomal tergum I; *TII*: metasomal tergum II.



Figs. 46-54. 46. *Paramasaris richardsi*, 14X. Dorsal view of scutellum and metanotum. 47. *P. cupreus*, 13X. Dorsal view of mesosoma. 48-49. Tegula. 48. *Gayella araucana*, 21X. 49. *G. reedi*, 15X. 50-52. Dorsal view of ♂ metasomal

in the *mutilloides* group (cf. Figs. 57–58 and 59–61, 63), and is here inferred as an elaboration. A sister-group relationship therefore obtains between *eumenoides* and *araucana*. The first has the autapomorphy of the humeri projecting above the anterior pronotal carina (Fig. 27). A very weak angle is also found in *reedi*, and *Paramasaris* has an angle of a different form (Fig. 24), but the projection is much stronger in *eumenoides*. Willink and Ajmat de Toledo (1979: fig. 3) depict *eumenoides* as having an apically bilobed aedeagus; however the shape varies among specimens in my dissections, and most have a broadly rounded apex as in other *Gayella* (Fig. 57). The sister-species of *eumenoides*, *araucana*, also has some autapomorphies. The acroglossal buttons are very reduced in size in the male, whereas they are elongate in the female and other *Gayella*. The pronotal punctation in *araucana* is relatively coarser than in the rest of the tribe, so this may also be a derived feature. The margins of the pronotum are more or less subparallel in *araucana* and more convex in other *Gayella* (cf. Figs. 27 and 28), but the difference from *eumenoides* is slight. The first metasomal tergum is narrower than in other species of the genus (cf. Figs. 43 and 44–45), but this is approached in some specimens of *eumenoides*. The male genitalia has the cuspis with the basal tubercle sharply pointed (Fig. 58). The tubercle is usually less pointed in *eumenoides* (Fig. 57), but some specimens approach *araucana*. Willink and Ajmat de Toledo (1979: fig. 5) depict a rather different digitus in *araucana*. However, their figures were evidently drawn from specimens flattened on slides, and do not accurately portray the relative uniformity in this structure (or the aedeagus) among the species (Figs. 57–63).

#### *Mutilloides* group

The most obvious feature supporting the monophyly of the *mutilloides* group is the coat of elongate black hairs (Figs. 36, 45, 53). This trait can be an ecological correlate in other vespids, being found for example in species of *Hypodynerus* (Eumeninae) sympatric with *Gayella*. Members of the *mutilloides* group share other

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tergum VII. 50. *G. reedi*, 17×. 51. *G. araucana*, 20×. 52. *G. eumenoides*, 17×. 53. *G. patagonica* ♂, 7×. Lateral view of metasoma. 54. *G. luispenai* ♂, 8×. Oblique ventral view of metasomal sternum II. *lm*: longitudinal metanotal carina; *sp*: sternal ridge projection; *sr*: posterolateral ridge of metasomal sternum II; *tm*: transverse metanotal carina.

derived features, however. The preoccipital carina is evanescent and separated from the postocular carina by more than an ocellar diameter in species of this group, whereas both are well developed and closely approximated in the *eumenooides* group and Euparagiinae. The femur is punctate in the *mutillooides* group; it is smooth in other gayellines. The spines defining the emargination of the last visible metasomal tergum are narrow and elongate in the *mutillooides* group (Fig. 50), whereas they are broader and shorter in the *eumenooides* group (Figs. 51–52). Since both states uniquely characterize monophyletic groups, the polarity cannot be clearly inferred. However, the state of the metasomal spines in the *mutillooides* group is a more extreme development, and is here suggested as relatively apomorphic.

Within the group, *reedi* is the sister-group to the remaining three species. I have not discovered any clear autapomorphies of this species. Synapomorphies uniting *patagonica*, *mutillooides* and *luispenai* include greater development of the long black hairs on the metasoma (extending over the disc of tergum II, Fig. 53), and an elongate malar space (length 1/2 to greater than the width of the interantennal distance, Fig. 14; shorter than this in other gayellines, Figs. 15–17). The postocular carina tends to be more effaced (as in Fig. 20), but traces appear to be present in some specimens. Metasomal sternum II in the male and to some extent also the female is bordered posterolaterally with blunt ridges (Figs. 53–54), however these are variably developed in *patagonica*, and *reedi* approaches this condition. Among these three species, the features I have polarized are autapomorphies. Hence, the relationships are at present unresolved (Fig. 2). Autapomorphies of the species are: for *mutillooides* the very long malar space (Fig. 14), the acroglossal buttons more elongate and the glossa more deeply bifid than other *Gayella*, and the cuspis tubercle quite blunt (Fig. 61); for *luispenai* the male metasomal sternum II projections elongate (Fig. 54); and for *patagonica* the female propodeal median groove narrowed before broadening dorsally (Fig. 55; smoothly narrowed in other *Gayella*, Fig. 45).

#### IDENTIFICATION KEYS

##### Genera

1. Pronotum with two transverse carinae (Figs. 29–31); clypeus emarginate to truncate (Figs. 11–13); last tergum neither

- emarginate nor bispinose apically . . . *Paramasaris* Cameron  
 – Pronotum with one carina (Fig. 7); clypeus pointed or rounded (Figs. 14–17); last tergum widely emarginate and bispinose apically (Figs. 50–52) . . . . . *Gayella* Spinola

*Paramasaris*

1. Pronotum with posterior carina extending no further dorsad than anterior carina (Fig. 24); head with carina not extending from vertex to mandibular base (Fig. 20); propodeum without oblique carinae (Fig. 41) (Brazil) . . . . . *richardsi* (Giordani Soika)
  - Pronotum with posterior carina extending much further dorsad than anterior carina (Figs. 25–26); head with carina extending from vertex to mandibular base (Fig. 19); propodeum with oblique carinae (Fig. 33) . . . . . 2
2. Pronotum with posterior carina incomplete dorsally (Fig. 25); female clypeus without lateral carinae (Fig. 12) (Argentina, Brazil) . . . . . *brasiliensis* Giordani Soika
  - Pronotum with posterior carina continuous dorsally (Fig. 26); female clypeus with lateral carinae (Fig. 13) . . . . . 3
3. Propodeum with median groove delimited by carinae which are higher than the adjacent areolae (Fig. 34); mesepisternum with dorsal groove narrower, shallow (Fig. 40) (Colombia, Peru) . . . . . *cupreus* Giordani Soika
  - Propodeum with median groove not delimited by carinae which are higher than adjacent areolae (Fig. 33); mesepisternum with dorsal groove broad, deep (Fig. 31); (Colombia to Mexico) . . . . . *fuscipennis* Cameron

*Gayella*

1. Thorax and metasoma with short, sparse whitish pubescence (Fig. 1) . . . . . 2
  - Thorax and at least TI, TII basally and sterna with long, thick black hairs (Fig. 36) . . . . . 3
2. Pronotum rounded laterally (Fig. 28) . . . . . *araucana* Willink
  - Pronotum angled laterally (Fig. 27) . . . . . *eumenoides* Spinola
3. Malar space as long as width of interantennal distance (♀, Fig. 14) or longer (♂) . . . . . *mutilloides* Saussure
  - Malar space less than the width of the interantennal distance . . . . . 4
4. TII with long hairs only anteriorly, posterior terga without long hairs (Fig. 36) . . . . . *reedi* Willink

- TII with long hairs extending to apex, posterior terga densely haired (Fig. 53) ..... 5
- 5. Male SII with blunt posterior projections (Fig. 54); female with propodeal median groove narrowing dorsally (fig. 45) ..... *luispenai* Willink & Toledo
- Male SII without projections (Fig. 53); female with propodeal median groove narrowed ventrally before broadening dorsally (Fig. 55) ..... *patagonica* Willink

## TAXONOMIC NOTES

Tribe Gayellini Bradley, 1922

Genus *Paramasaris* Cameron, 1901:311. Type species *Paramasaris fuscipennis* Cameron, 1901. Monotypic.

*Zethoides* Cameron, 1904: 93. Type species *Zethoides flavolineatus* Cameron, 1904. Monotypic. *Non Zethoides* Fox, 1899.

*Plesiozethus* Cameron, 1905:269. Replacement name for *Zethoides* Cameron.

*Metazethoides* Schulz, 1906:213. Unnecessary replacement name for *Zethoides* Cameron.

*Paraguayella* Giordani Soika, 1974:87, 89, 99. Type species *Paraguayella richardsi* Giordani Soika, 1974. Original designation. NEW SYNONYMY.

*Paramasaris richardsi* (Giordani Soika),

NEW COMBINATION

*Paraguayella richardsi* Giordani Soika, 1974:101, fig. 2, pl. II, ♀ (BMNH)—“Brasile: Mato Grosso, Serra Roncados, R. S. Base Camp.”

In his description, Giordani Soika referred to 13 specimens; however I have seen only four specimens in the British Museum. The holotype is on a pin with a paratype, which is not mentioned in the description. The holotype label is above the paratype label, and so the upper specimen is presumably to be treated as the holotype.

In addition to the material in the British Museum, I have seen female specimens from the following localities in Goias in Brazil: “24 kil. E. Formoso, June 6, 1956 (F. S. Truxal)” UCD; “S. Isabel do Morro, Ilha do Bananal, June 1961 (M. Alvarenga)” MCZ.

*Paramasaris brasiliensis* Giordani Soika

*P. brasiliensis* Giordani Soika, 1974: 105, ♀♂ (type ♀ MCZ) —“Brasile: Nova Teutonia, Santa Catarina.”

Giordani Soika cited the holotype and allotype as deposited in the USNM, but both are in fact in the MCZ, along with the paratype collected on I-1967. I have seen additional specimens, both in the collection of UCD, from “Brazil: Nova Teutonia, Santa Catarina, I 1965 (F. Plaumann)”; and “Argentina: Haut Parana, Thu-Cuare prés San Ignacio, 1911 (E. R. Wagner)”.

*Paramasaris cupreus* Giordani Soika

*P. cupreus* Giordani Soika, 1974: 106, ♀ (BMNH)—“Columbia: Caqueta, Florencia, 480 m.”

Besides the holotype one of the paratypes mentioned by Giordani Soika is in the British Museum. New localities in Colombia include: “Putumayo, Mocoa, 30.X.1974 (M. Cooper)” now in the MCZ; “Dept. Magdalena, Socorpa Mission, Sierra de Perija, VIII.5-25.1968 (Borys Malkin)” 3 ♀ AMNH and MCZ. One of the Magdalena specimens is labelled “1500m.” The specimen from Mocoa has a label reading “collecting mud in forest.” I have also seen a specimen from “Peru: Loreto, Pucallpa 10.iv.1965 (J. M. Schunke)” BMNH.

Giordani Soika (1974) alluded to various differences in sculpture between *cupreus* and *fuscipennis* in his description, but several of these do not hold up in the additional material I have seen. The pronotal carina and tergal punctation are similar in most specimens, and the clypeus is not more narrowly emarginate in *cupreus*. The finer and sparser punctation on the dorsum of the mesosoma in *cupreus* is usually consistent, particularly the pronotum, but one of the Magdalena specimens has the punctures on the scutum and scutellum about as in *fuscipennis*.

*Paramasaris fuscipennis* Cameron

*P. fuscipennis* Cameron, 1901: 312, ♀ (BMNH)—“Santa Fé Mountains, New Mexico.”

*Zethoides flavolineatus* Cameron, 1904: 94, ♂ (BMNH)—“Panama (Pacific side).”

The statement of the type locality as being in New Mexico is perhaps an error. As Bradley (1922:387) put it: "I have not been able to learn of any mountains bearing this name." There is a Santa Fé mountain in Jalisco in Mexico (20° 30'N, 103° 02'W), and this species has been later collected in other parts of Mexico, but never in the United States. Krombein (1979) did not include this species in the revised Catalog of Hymenoptera north of Mexico. Besides the types, I have seen specimens from Guatemala: S. Geronimo (Champion) (BMNH and one now in MCZ); "Mexico: Jalisco, Chamela, IX-26-1985, ex. *Nissolia* (R. J. McGinley)" USNM; "Sinaloa, 5 mi. NW Choix, VIII-27 and 31, and IX-5-1968 (T. A. Sears, R. C. Gardner & C. S. Glaser)" UCD and MCZ. It has also been recorded from Colombia: Bogotá by Zavattari (1912; confirmed by Giordani Soika, 1974).

Genus *Gayella* Spinola, 1851: 328. Type species *Gayella eumenoides* Spinola, 1851. Monotypic.

*Eumenoides* group  
*Gayella eumenoides* Spinola

*G. eumenoides* Spinola, 1851:333, pl. II, fig. 2, ♂♀ (lectotype ♂ MNHN, designated by Giordani Soika, 1974:98)—Chile, "provincias del norte y sobretudo en Santa Rosa."

*G. sicheliana* Schulthess, 1910: 189. As a synonym of *eumenoides*, attributed to Saussure.

Common in central Chile, this species has also been recorded from Argentina: Mendoza by Brèthes (1903) and following him various authors; however, Willink (1956) considered this record dubious. I have seen specimens from Aconcagua, Atacama, Coquimbo, Curicó, Maule, O'Higgins, Santiago and Valparaíso.

Bequaert and Ruiz (1942) summarized early literature on this species. Reed (1893) pointed out that Spinola had confused the sexes in the original description, and Willink (1956) observed that Spinola and Saussure confused *eumenoides* and *araucana*. This is the only gayelline for which any behavioral information has been published, by Claude-Joseph (1930). It provisions clusters of free mud cells with nectar.

*Gayella araucana* Willink

*G. araucana* Willink, 1956:341, 342, 346, figs. 3, 4, ♀♂ (type ♀ IPC)—"Chile, Prov. Santiago: Renca."



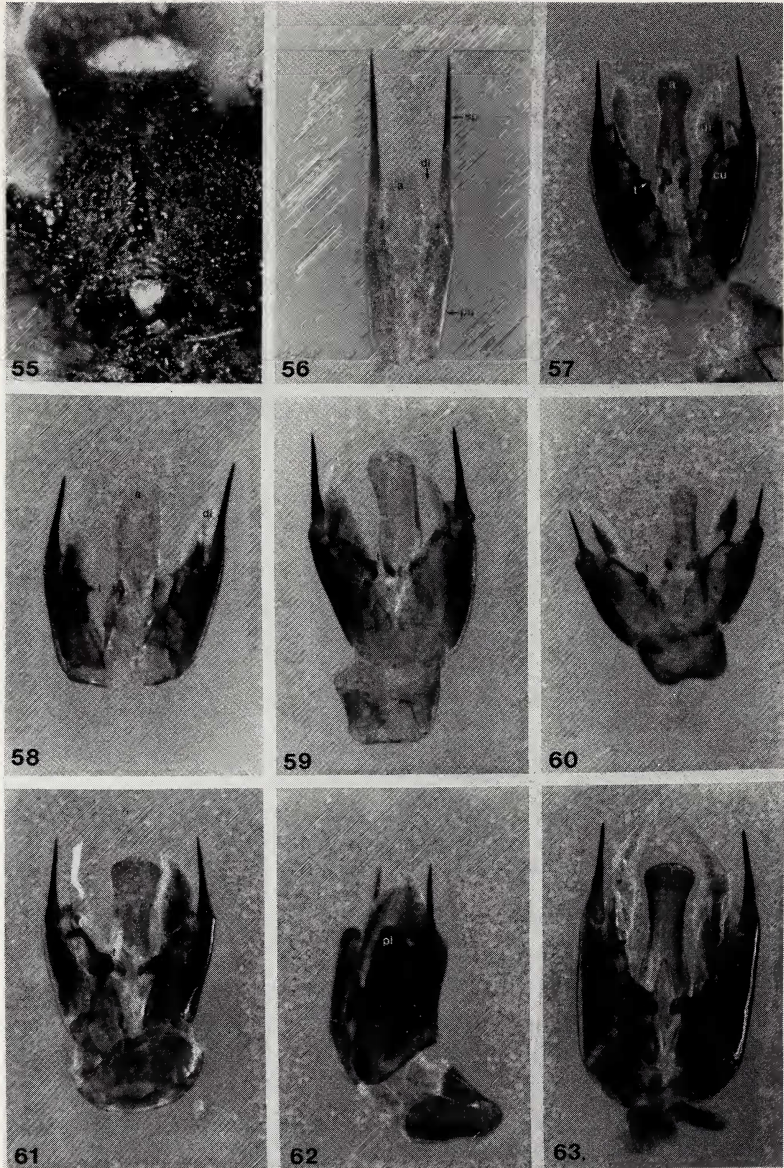
I have seen specimens from Aconcagua, Atacama, Coquimbo, O'Higgins, Santiago (including paratypes from BMNH and IML) and Talca. Willink and Ajmat de Toledo (1979) recorded this species from Bio-Bio.

Willink and Ajmat de Toledo (1979) recognized the same species groups as the present paper, but stated that *araucana* is the most distinct and should possibly be treated as a different genus. They even stated that morphologically it approaches eumenines of the genera *Ancistrocerus* and *Stenodynerus*, but it does not possess any of the synapomorphies of that subfamily (Carpenter, 1981). The characters cited as distinguishing *araucana* are only trivially different from other *Gayella*. These characters comprise the mesosoma with lateral margins subparallel, the malar space nearly obliterated, the form of the emargination of male metasomal tergum VII and the form of the male genitalia. The condition of the malar space is primitive, and similar to *eumenoides* (cf. Figs. 15 and 16); the emargination of male tergum VII is little different from that of *eumenoides* (cf. Figs. 51 and 52). As noted above, their figures of the male genitalia are misleading; *araucana* is no more different in the digitus or aedeagus than the other species are from each other (Figs. 57-61, 63). The cuspis is autapomorphic in having a sharp tubercle, but this again is not properly illustrated in the other species, all of which have some projection. The subparallel mesosoma is also autapomorphic, but this is a minor difference compared to the outstanding similarities shared by all species of *Gayella*. Placement of *araucana* in a separate genus would render *Gayella* paraphyletic, which is reason enough to reject doing so.

*Mutilloides* group  
*Gayella reedi* Willink

*G. reedi* Willink, 1963:385, 1 fig., ♀ (CAS)—"Casa Blanca, Valparaíso, Chile."

I have seen material from Atacama, Coquimbo (including a USNM paratype) and Valparaíso (including CAS and IML paratypes). The male has not previously been described. One specimen labelled "Chile, Coquimbo: Llano de la Higuera, N. of La Serena, Sept. 29, 1980 Luis E. Peña" AMNH, and two from "Chile: Atacama 20 km. E on Ruta 31 nr. Puquios, 9-X-1984 (C. Porter & T. O'Neill)" CP and MCZ, evidently belong to this species. The pilosity is the same as in the female (Fig. 36). The color markings are also



Figs. 55-63. 55. *Gayella patagonica* ♀, 11X. Posterodorsal view of propodeum. 56-63. Male genitalia. 56-61. Ventral view. 56. *Paramasaris fuscipennis*, 26X. 57. *G. eumenoides*, 17X. 58. *G. araucana*, 21X. 59. *G. reedi*, 18X. 60. *G. pata-*

identical, except that the clypeus is whitish (Fig. 17); the scutellum is completely black (often with some white in females). The clypeus is longer than wide and weakly pointed, the mandibles are tridentate, the postocular carina is very short, the malar space is about 1/2 the width of the interantennal distance, the pronotum projects very slightly, the first metasomal tergum is about 1 1/3 as long as wide, and sternum II has traces of posterolateral ridges. The genitalia are illustrated in Fig. 59.

#### *Gayella mutilloides* Saussure

*G. mutilloides* Saussure, 1855: 114, ♀ (BMNH)—“Le Chili.”

*G. odyneroides* Schulthess, 1910: 189. *Lapsus* for *mutilloides*.

*G. mutilloides nigerrima* Giordani Soika, 1960 (1958): 80, ♀ (Giordani Soika coll.)—“Cile.”

The synonymy was established by Bequaert and Ruiz (1942) and Willink (1963). Willink (1956) described the male, and recorded the species from Argentina: Chubut and Neuquén. In addition to the holotype of *mutilloides*, I have seen material from Chile: Ñuble, ?Valdivia (CAS), and “El Manzano” (MCZ); and Argentina: Rio Negro. It has also been recorded from Aconcagua and Malleco by Willink and Ajmat de Toledo (1979).

#### *Gayella patagonica* Willink

*G. patagonica* Willink, 1956:341, 342, 350, figs. 9, 10, 11, ♀♂ (type ♀ IML)—“Esquel, Chubut, Argentina.”

*G. cerceroides* Giordani Soika, 1960 (1958):82, ♀ (BMNH)—“N. W. Patagonia, 1000–3000 piedi.”

The synonymy was established by Willink (1963), who also recorded this species from Chile: Lo Valdés, Cordillera de Santiago 2500 m (stated to be in the MCZ but not there; Willink and Ajmat de Toledo, 1979, cite what is evidently this specimen as in IML). In addition to the holotype of *cerceroides*, I have seen specimens from Argentina: Chubut (including a paratype from MF) and Rio Negro,

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*gonica*, 11×. 61. *G. mutilloides*, 13×. 62. *G. mutilloides*, 13×. Lateral view. 63. *G. luispenai*, 15×. Ventral view. *a*: aedeagus; *di*: digitus; *cu*: cuspis; *ng*: narrowing of propodeal median groove; *pa*: paramere; *pl*: dorsal parameral lobe; *sp*: parameral spine; *t*: tubercle of cuspis.

as well as the BMNH paratypes from "N. W. Patagonia." Willink and Ajmat de Toledo (1979) also mention a Mendoza record.

*Gayella luispenai* Willink and Ajmat de Toledo

*G. luispenai* Willink and Ajmat de Toledo, 1979: 427, 428, 429, figs. 1, 6, 7, ♂♀ (type ♂ IML)—"Riconada, Jujuy, Argentina."

I have seen two specimens, a male from Jujuy, Est. Iturbe 17-I-1979 (L. Fidalgo) and a female from Mendoza, Uspallata 5.XII.1979 (A. Roig). This species was also recorded from Bolivia: Potosí by Willink and Ajmat de Toledo (1979).

This species is very similar to *patagonica*, as noted by Willink and Ajmat de Toledo (1979:430). Most of the characters they cite will not distinguish females. The series of *patagonica* I have seen from Rio Negro (MF) overlaps in size, length of the malar space and development of protuberances on female metasomal sternum II. The punctuation tends to be less coarse on the scutellum of *patagonica*, but this varies among the specimens. The propodeal median groove will separate them (Figs. 45, 55), but as I have seen only one female of *luispenai*, I cannot be certain that this feature does not vary. Males are readily distinguished by the sternal projections in *luispenai* (Fig. 54).

#### BIOGEOGRAPHY

It is clear from the few records for some species that their distributions are very poorly known, and further collecting, particularly of *Paramasaris*, will doubtless extend the ranges of some of these. Nevertheless, a few remarks about biogeography may be made. *Paramasaris* and *Gayella* occupy completely different regions, Tropical American versus Patagonia, which corresponds to a well-known vicariant break. Within *Gayella*, most of the species overlap broadly in distribution. The clade *mutilloides* + *patagonica* + *luispenai* is the only group which occurs on the eastern side of the Cordillera, but the first two species are also found in Chile. By contrast, *Paramasaris* shows a pattern of endemism. Within the genus, the distribution of the sister-species *fuscipennis* and *cupreus* is basically trans-Andean: Central America versus western Amazonia. There is a record of *cupreus* from the western side of the Sierra de Perijá, but this was elevated in the late Oligocene (Kellogg, 1984). In turn, the sister-group of this clade, *brasiliensis*, is southeastern Brazil, and the sister-group of all three species, *richardsi*, is southern Amazon

basin. This pattern does not correspond to that shown by the avifauna, for example Cracraft and Prum (1988), where southeastern Brazil is not closely related to a western Amazon/trans-Andean clade. However, that study showed southeastern Brazil as a composite area, implying either dispersal or differing ages for components of the regional biota. The latter factor may well explain the incongruence; Gayellini is an ancient group, since the Masarinae as a whole is gondwanian (Carpenter, 1981).

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#### SUMMARY

The phylogenetic relationships of the gayelline wasps are investigated using cladistic methods. *Paragayella* is the sister-group of *Paramasaris*, and is synonymized with that genus. This taxon is the sister-group of *Gayella*. Cladograms are presented for the species in each genus, along with keys and distributional notes.

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